FACTORS AFFECTING THE DISTRIBUTION OF PONDEROSA AND JEFFREY PINES IN CALIFORNIA

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Pinus ponderosa Dougl. and *P. jeffreyi* Murr. are among the most widely distributed forest trees in California and are well known to western botanists. They are very closely related, and various authors have treated them either as species (Sudworth, 1908; McMinn, 1951) or as varieties of a single species (Shaw, 1914; Jepson, 1925). However, after extensive field investigations (Haller, 1957) the details of which will be published elsewhere, I am convinced that *P. ponderosa* and *P. jeffreyi* are well defined species, and I shall treat them as such in this paper. All of the observations which follow are my own, unless otherwise noted, and were made in connection with the taxonomic study referred to above.

In California, *Pinus ponderosa* occurs from the Oregon border south along the Cascade Range and the western slope of the Sierra Nevada in an uninterrupted belt over 400 miles long and about 25 miles in width. Throughout this belt *P. ponderosa* is a conspicuous element in a forest rich in coniferous species. It is also common on the higher coastal-facing slopes of the mountains of southern California as far south as Cuyamaca Lake in San Diego County, and occurs sporadically in the Coast Ranges, especially north of San Francisco Bay.

The distribution of *P. jeffreyi* roughly parallels that of *P. ponderosa* in California, but *P. jeffreyi* is relatively more abundant in the south, and extends beyond the range of *P. ponderosa* into the higher mountains of northern Baja California, Mexico.

Although the ranges of *P. ponderosa* and *P. jeffreyi* in California nearly coincide in the broadest geographical sense, and although both are often found at the same locality, the two species characteristically occupy different habitats. *Pinus ponderosa* occupies the lower coastal-facing slopes of the mountains, whereas *P. jeffreyi* is usually found on the higher coastal or desert-facing slopes. The altitudinal ranges of *P. ponderosa* and *P. jeffreyi* shift gradually higher from north to south in California, just as do vegetation zones in general. However, the degree of shifting is not the same in both species. The lower limit of the *P. ponderosa* zone rises steeply from north to south. In the north, near Mount Shasta, the lower limit of *P. ponderosa* is about 1000 feet, but in the south, near Barton Flats in the San Bernardino Mountains, it is at 5000 feet (fig. 1). The upper limit of the *P. ponderosa* zone does not rise as steeply. It changes from about 5000 feet in the north to 7000 or 7500 feet in the south. Therefore, the altitudinal range of *P. ponderosa* contracts from about 4000 feet near Mount Shasta to little more than 2000 feet at Barton Flats. South of the Barton Flats area *P. ponderosa* becomes rapidly more infrequent in the

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montane forest, until the most southerly stand is reached at Cuyamaca Lake, at the unusually low altitude of 4600 feet.

The lower edge of the *P. jeffreyi* zone rises from about 5000 feet near Mount Shasta to only a little over 6000 feet near Barton Flats (fig. 1). The zone in which *P. ponderosa* and *P. jeffreyi* overlap is consequently broader in the south than in the north, and stands comprised of both species are extensive near Barton Flats but highly restricted near Mount Shasta (Wiggins, 1940 and my own observations).[1] However, there are numerous localities throughout the state such as Shasta Valley in Siskiyou County and Pine Valley in southern San Diego County where *P. jeffreyi* occurs much lower, either with or without *P. ponderosa,* in what would usually be the lower portion of the *P. ponderosa* zone. The upper limit of *P. jeffreyi* rises from about 7500 feet near Mount Shasta to 9500 or 10,000 feet near Barton Flats. Thus the normal altitudinal range of *P. jeffreyi* increases from about 2500 feet in the north to 3500 or 4000 feet in the south.

What are the factors that cause this narrowing of the altitudinal range of *P. ponderosa* and broadening of the altitudinal range of *P. jeffreyi* in the south? There is both experimental and observational evidence which indicates that moisture at the lower altitudinal limit and temperature at the upper limit are usually the critical factors. Daubenmire (1943) has shown experimentally that seedlings of several important species of Rocky Mountain conifers, including *P. ponderosa,* are capable of withstanding much higher soil temperatures than those in their natural environments, but that they quickly succumb to drought conditions more severe than those in their natural habitats. In most areas of California also, *P. ponderosa* is probably restricted at its lower limit by moisture rather than temperature or some other factor. *Pinus ponderosa* is rarely found in areas with less than 25 inches of annual precipitation except near permanent sources of water. Of course moisture alone may not always be the limiting factor at low elevations. For example, in some localities where precipitation is still adequate but almost limiting, *P. ponderosa* might be held in check by its inability to compete with the more xeric chaparral vegetation. Billings (1950) has described the interesting occurrence of *P. ponderosa, P. jeffreyi* and other montane coniferous species on chemically altered andesitic soils in western Nevada. The climate of the area is too arid for these species under normal soil conditions, and supports only sagebrush or piñon-juniper vegetation. However, the sagebrush and most other shrubs cannot tolerate the chemically altered soils, and Billings has concluded that the absence of shrubby competitors enables the pines to persist.

The upward migration of *P. ponderosa* is, in all probability, usually

[1] Professor G. Ledyard Stebbins (personal communication) has observed extensive mixed stands of *P. ponderosa* and *P. jeffreyi* in the North Coast Ranges. The stands in this area apparently comprise an exception to the usual pattern of restricted mixed stands in the north and extensive ones in the south.

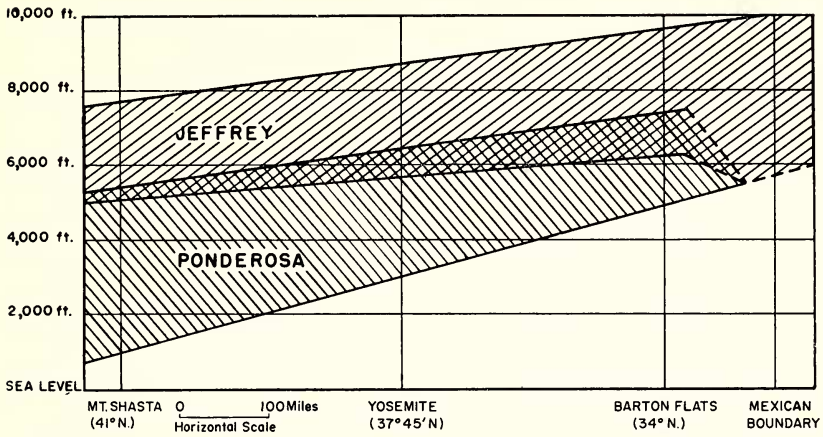

FIG. 1. Altitudinal distribution of *Pinus ponderosa* and *P. jeffreyi* along a north-south transect in California.

checked by low temperature. Californian *P. ponderosa* is killed by freezing when grown in areas with low winter temperatures, such as the Rocky Mountains (Weidman, 1939). I have observed frost damage on young individuals of *P. ponderosa* in California after periods of severe cold. The limiting effect of the low temperature undoubtedly works on the seedlings or young trees, because mature stands of *P. ponderosa* at its upper altitudinal limit are vigorous and show no evidence of being stunted.

Assuming that moisture and low temperature are the principal limiting factors for *P. ponderosa* at its lower and upper limits respectively, it is apparent from climatic data why *P. ponderosa* has a narrower altitudinal range in the south than in the north. As one travels south in California, precipitation generally decreases more rapidly than temperature increases at any given altitude (U.S. Weather Bureau, 1958). In other words, the isohyets gain altitude faster than the isotherms toward the south, leaving an ever shrinking zone that is favorable to the growth of *P. ponderosa*. It might be wondered, if the above is true, why *P. ponderosa* stops so abruptly in San Diego County rather than continuing toward the south over a decreased altitudinal range. There is no abrupt environmental shift at Cuyamaca Lake, and there are sites farther south that appear to be capable of supporting *P. ponderosa*. The reasons for the relatively sharp southern limit of the species may be historical. For example, a severe drought could have eliminated *P. ponderosa* south of where it occurs now, and the species may not yet have had sufficient opportunity to expand and reach its former extent.

Pinus jeffreyi is probably limited at the upper margin of its altitudinal range by a complex of factors all basically caused by low temperatures. Individuals growing near the upper limit of the species are often severely stunted in appearance, and obviously are showing the effects of the harsh

climate. In addition, the upper limit of *P. jeffreyi* almost exactly parallels that of *P. ponderosa* from north to south in California, suggesting that different degrees of the same factors are limiting both species at the upper margins of their altitudinal range (fig. 1).

The lower altitudinal limit of *P. jeffreyi* does not appear to be determined by any obvious physical factors, but rather by competition with *P. ponderosa* or other species. *Pinus ponderosa* grows faster under cultivation than *P. jeffreyi* in many diverse localities, from the Institute of Forest Genetics at Placerville, California (within the range of *P. ponderosa*), to England (Hooker, 1884). Near its upper limit *P. ponderosa* may not grow much faster than *P. jeffreyi* and thus permit the occurrence of mixed stands, but lower down, the more vigorous growth of *P. ponderosa* could exclude *P. jeffreyi* since both species have about equally high light requirements (Sudworth, 1908). The much greater extent of stands containing both species in southern California than farther north might be due to a slightly lowered vigor and subsequent lessening of the competitive ability of *P. ponderosa* in the south. In relatively dry southern California, *P. ponderosa* is in an environment where moisture is more likely to be limiting than in the north, and therefore might be expected to be less vigorous. The occurrence of *P. jeffreyi* in areas where *P. ponderosa* is lacking is further evidence of the limitation of *P. jeffreyi* by competition. In southern San Diego County, beyond the southern limit of *P. ponderosa, P. jeffreyi* often occurs through the entire altitudinal range of the montane forest. A short distance to the north, the lower portions of this forest are occupied by *P. ponderosa* instead. In the Sierra Nevada there are numerous sites within the montane forest, often at very low altitudes, such as sandbars in rivers or areas of serpentine soil, where *P. ponderosa* occurs infrequently if at all. The less demanding *P. jeffreyi,* however, is frequently encountered on these sites.

Revealing evidence concerning the distribution limits of *P. ponderosa* and *P. jeffreyi* has been obtained from east-west transects across the mountains as well as by north-south transects along their axes. As an example, I shall describe a west to east transect across the Sierra Nevada in the vicinity of Yosemite National Park in central California. The western and eastern slopes of the central portion of the Sierra Nevada display a striking series of contrasts, both topographically and climatologically. The western slope is fairly gradual, receives from 30 to 60 inches of precipitation annually in the montane forest belt (U.S. Weather Bureau, 1958), and has a relatively mild climate characterized by temperature extremes that are not pronounced. The eastern slope, on the other hand is very precipitous, receives only 10 to 20 inches of annual precipitation in the montane forest belt because of the rain shadow effect produced by the 13,000 foot crest that lies to the west, and has a continental climate with great extremes of temperature.

At the latitude of Yosemite (38° N.), the lowest continuous stands of *P. ponderosa* appear at an elevation of about 3000 feet, where the mean

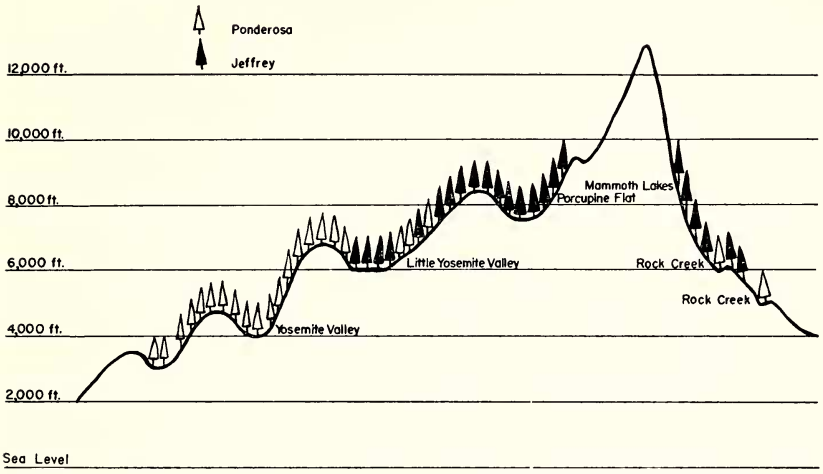

FIG. 2. Altitudinal distribution of *Pinus ponderosa* and *P. jeffreyi* along an idealized west-east transect across the central Sierra Nevada. Open triangles represent *P. ponderosa*; solid triangles represent *P. jeffreyi*.

annual precipitation is at least 30 inches. At about 6000 feet, *P. jeffreyi* is first found in abundance. The stands of *P. jeffreyi* growing at this relatively low altitude are usually not scattered at random over the slopes, however, but are concentrated near the margins of meadows or along streams, together with *Pinus contorta* subsp. *murrayana* Engelm., which occasionally occurs below its usual range in such places. *Pinus ponderosa* remains abundant for several hundred feet above the low places where *P. jeffreyi* is first encountered, especially on south-facing slopes, before giving way to *P. jeffreyi*. Above 6500 or 7000 feet, *P. jeffreyi* occurs alone and continues up to an elevation of approximately 9000 feet (fig. 2).

If the transect is continued across the 13,000 foot crest to the more arid eastern slope of the Sierra Nevada, *P. jeffreyi* will again be found below the 9000 foot elevation. Below 7000 or occasionally 6000 feet, where the annual precipitation may be as low as 10 inches, *P. jeffreyi* gives way to more xeric species, such as *Pinus monophylla* Torr. and *Artemisia tridentata* Nutt. *Pinus ponderosa* is not at all common on the eastern slope, and occurs without exception only along the banks of a few perennial streams. It is most abundant along Rock Creek near the Inyo-Mono county line at altitudes ranging from 5000 to 6500 feet (fig. 2).

The distribution pattern of *P. ponderosa* and *P. jeffreyi* along this west to east Sierran transect appears to be the result of the same limiting factors as those suggested by their north-south distribution. Although the lowest extensive stands of *P. jeffreyi* on the western slope of the Sierra Nevada are usually near meadows or along streams, the trees are prob-

ably not there because they need the moisture, but rather because *P. jeffreyi* is more tolerant of cold than is *P. ponderosa*. These low pockets where *P. jeffreyi* occurs are colder than the surrounding slopes in winter. The occasional presence of the usually subalpine *P. contorta* subsp. *murrayana* in these pockets is further evidence of this fact. Probably *P. jeffreyi* merely tolerates the extra moisture present at its lowest localities, because, as already noted, the species occurs in much drier localities in other areas. In the harsh climate of the eastern slope of the Sierra Nevada, *P. ponderosa* survives only at low elevations where it is not too cold and along streams where it is not too dry. Where *P. ponderosa* and *P. jeffreyi* are found in the same general area on the eastern slope, the latter, in contrast to *P. ponderosa* often occurs both near the streams and on the adjacent slopes.

Pinus ponderosa is found in abundance on both sides of the Sierra crest from Lake Tahoe northward. However, in this region the crest of the range is much lower than farther south, and the environmental differences between the western and eastern slopes are not nearly as great. On the desert-facing slopes of the higher mountains of southern California, *P. ponderosa* is again restricted to unusually moist localities.

SUMMARY

Pinus ponderosa and *P. jeffreyi* are important components of the California montane forest. *Pinus ponderosa* generally occurs on the lower coastal slopes, while *P. jeffreyi* generally occurs on the higher coastal or interior slopes. The distribution of *P. ponderosa* is usually checked by lack of moisture at low altitudes and by low temperature at high altitudes. *Pinus jeffreyi* is also limited by low temperature at high altitudes, but at its lower margin the distribution of the species is apparently limited primarily by competition with *P. ponderosa*. The extensive mixed stands of *P. ponderosa* and *P. jeffreyi* in southern California where *P. ponderosa* may be less vigorous than in the north, might be the result of decreased competition from *P. ponderosa*. *Pinus jeffreyi* is more tolerant of extremes of low temperature and aridity than is *P. ponderosa*, and is at least equally as tolerant as *P. ponderosa* of extremes of high temperature and high moisture.

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VIVIPARY IN CORDYLINE AUSTRALIS HOOK.

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Vivipary is defined by Jackson (1928) as ". . . . germinating or sprouting from seed or bud, while attached to the parent plant." Examples of vivipary are known in a number of genera of both the monocotyledons and dicotyledons. The classical example of this condition occurs in such mangroves as *Rhizophora mangle* Blanco. In this species when the seed germinates while still attached to the parent plant, the hypocotyl-radical elongates, forming a long sharp structure (Daubenmire, 1947, fig. 10, p. 64). When this seedling structure becomes heavy enough, it breaks away from the parent plant and drops into the mud below. Because this sharp hypocotyl-radical structure penetrates the mud the seedling often becomes anchored and is prevented from being washed away from its environment, especially in the intertidal zone.

In the Agavaceae of Hutchinson, of which *Cordyline* is one member, several genera have been reported to show vivipary. Both *Agave* and *Furcraea* are included in this category. The viviparous condition in *Furcraea* is a great deal different than that of *Rhizophora* or *Cordyline*. In *Furcraea* at certain points along the inflorescence bulbils are formed. These bulbils (aerial deciduous buds) consist of a series of papery and photosynthetic bud scales surrounding a short axis and a shoot apex. These structures are often formed in enormous numbers and literally cover the ground when they abscise from the parent inflorescence. Bulbils begin to grow immediately when proper conditions prevail; plants produced in this manner have a very rapid rate of early growth.

In a cultivated plant of *Cordyline australis* Hook. growing in Berkeley, California, many cases of vivipary were observed. The bright-green young seedlings were easily seen protruding out of the white fruits. A total of over fifty separate fruits were found exhibiting this character.

In most cases the cotyledonary arch and the first leaf were all that could be seen of the seedling outside the fruit. Two cases were observed in